

THE DEVELOPMENT OF GONIONEMA MURBACHII.

BY HENRY FARNHAM PERKINS.

Gonionemus A. Agassiz, 1862, Contrib. Nat. Hist. U. S., IV, p. 350.

From γωνιο, angled, and νημα, thread, "kneed tentacles."

Gonyonema Haeckel, 1879, System der Medusen.

Gonionemus Murbach, 1895, Journal Morph., XI, 2.

Gonionemus Murbachii Mayer, 1901, Brooklyn Inst. Sci. Bul., I, 1.

Gonionema A. Agassiz, MSS.

Gonionema Murbachii Perkins, Johns Hopkins Un. Cir., May, 1902.

INTRODUCTION.

The genus *Gonionema* was established by Dr. Alexander Agassiz to include a medusa which he discovered in 1862 in the Gulf of Georgia, Washington Territory. Its most striking character, anatomically, is the peculiar form of the tentacles, which are bent at an angle near the tip, and at the angle bear a sucking organ by means of which the medusa makes itself fast to any favorable object. This peculiarity in the form of the tentacles suggested to Agassiz the name which he proposed. The form of the name which is now used is that which Dr. Agassiz offers in correction of the original one, which was in error as to its ending.

For a long time the Gulf of Georgia was the only locality from which this genus was described. In 1894, however, another habitat was discovered far distant, at Woods Hole, Massachusetts. Since then members of the genus have been found at the widely separated localities of the Fiji Islands and Alaska. A closely allied genus has been described from the coast of Brazil and from the Bahamas. Mayer says that he found a new species of *Gonionema* ("aphrodite") in the Bahamas, but as a matter of fact this medusa possesses rather the characters of the Olindiadæ, two distinct kinds of tentacles and papilliform gonads.

The history of the Woods Hole *Gonionema* is interesting. In spite of the fact that the "eel-pond" at the centre of the village of Woods Hole, a small body of water connected with the outer harbor by a narrow inlet, is easy of access to collectors, and that numerous students of jelly-fishes had investigated the waters around

Woods Hole summer after summer for a number of years, *Gonionema* was never found in the Atlantic Ocean until 1894. During that summer a number of specimens were taken from the eel-pond, the creature having made an astonishingly sudden appearance upon the scene. It seems incredible that *Gonionema* could have been living in this small body of water for any time previously, or at any rate that any number of individuals had been there. But the jelly-fish at once secured a good "foothold," and since the first summer it has been very plentiful; its numbers remain undiminished by the wholesale raids of collectors, in spite of the keen anxiety of some of those interested in it. During the summer of 1894, when *Gonionema* was first found at Woods Hole, Prof. W. K. Brooks secured a number of specimens and made drawings both from live medusæ and from sections of preserved material. Some of these drawings, Pl. XXXIII, figs. 21, 22, Pl. XXXIV, fig. 25, are now published, with Dr. Brooks' generous permission, for the first time.

The first printed account of the Woods Hole species of *Gonionema*, since recognized as distinct from the *G. vertens* of Agassiz, was published in 1895 by Dr. L. Murbach.¹ In several instances the species has been mentioned as identical with *G. vertens*, and it was not until 1901 that the specific name *Murbachii* was bestowed upon it by Dr. A. G. Mayer.

The work which I have done on the life-history of this form was originally undertaken and has since been prosecuted with Dr. Murbach's kind encouragement, and I have received from him many favors in the way of material and helpful suggestions. The research has been carried on during 1900 and 1901 at the U. S. Fish Commission Laboratory, where I have had the great privilege of working during the summer, and under the direction of Prof. W. K. Brooks at the Biological Laboratory of the Johns Hopkins University. I wish to acknowledge my obligations to Dr. Bumpus, Dr. H. M. Smith and Dr. Whitman for courtesies which they have extended to me in my work.

NOTE ON THE ONTOGENY OF THE "TRACHOMEDUSÆ."

According to Haeckel's classification *Gonionema* falls into his third order, the "Trachomedusæ." Haeckel characterized this

¹ L. MURBACH, 1895, "Preliminary Note on the Life-History of *Gonionemus*," *Journal of Morphology*, XI, 2.

order as follows: "Development, hypogenesis (not metagenesis), but usually with metamorphosis." Subsequent research into the life-history of this group has shown that each clause of this statement is open to emendation. In the first place, the "usually" is superfluous. The exceptions which Haeckel supposed to exist and which caused him to say "usually with metamorphosis" have been shown to be no exceptions, but cases of somewhat easily misunderstood metamorphosis. Such, for example, was the case of *Iriope*, which has been studied by Metschnikoff² and Brooks.³ The larva is a true hydra, although its free swimming mode of life and its superficial aspect caused it to be mistaken, formerly, for a gonosome. My study of a jelly-fish which Haeckel includes in his order "Trachomedusæ" leads to the conclusion that the first part of Haeckel's statement also requires revision, and that *metagenesis does occur* among medusæ of this order. Although there may be different interpretations of the terms "metagenesis" and "hypogenesis," the following notion of the process of alternation of generations may be safely accepted as that which is generally held by students of this group. The production by a larva of offspring unlike itself, and its own ultimate death without undergoing metamorphosis, are frequent accompaniments of the intermediate as of the primary process of multiplication; but they are by no means essential to the process of metagenesis or alternation of generations. Creatures which multiply sexually at one point of their life-history, and at another point non-sexually by budding or fission, are said to have a metagenetic development. In *Gonionema* a large number of adult individuals are produced from a single egg through an intermediate process of multiplication (text-figs. 2-10); buds are developed upon the body of the hydra-like larva, become detached and, beginning as planulæ, follow exactly the same course of development as the sexually produced parent. Both parent and offspring later change into fully developed medusæ. *Gonionema* has, then, a metagenetic form of development. It is, of course, a mistake to regard the mere presence of a hydrula stage enough to constitute alternation of generations (Murbach, 1895, p. 496).

These emendations of Haeckel's description of the order add

² METSCHNIKOFF, *Embryologische Studien an Medusen*, 1886.

³ BROOKS, *Life-History of the Hydromedusa*, 1886.

evidence to that already put forward by Brooks (1886, p. 300), and others, to show that the hard and fast lines drawn by Haeckel and the Hertwigs separating the "Trachilinæ" and the "Leptolinæ," on the ground of anatomical differences or developmental features, are not borne out by the facts. The Hertwigs (1878) hold that "the marginal sense organs (Gehörorgane) alone furnish characteristics which enable us in every case to distinguish the Trachomedusæ (Trachomedusæ and Narcomedusæ of Haeckel) from the Vesiculatæ (Campanularian medusæ) without knowledge of their development." Dr. Brooks has, however, described a species of *Laodice* which unites in its anatomical features the characters of both the Leptolinæ and the Trachylinæ, having the ocelli of the former order and the chitinous gonangium containing medusa buds,⁴ while Prof. Brooks has demonstrated (1886) that it also possesses the true endodermal sense clubs of the Trachylinæ.

It may be that the present record of observations on *Gonionema* will be of interest as contributing some new points to the present meagre knowledge of the manifold forms and types which are exhibited in the developmental processes of this great group.

GONOSOME.

Gonionema is a very attractive feature of the Woods Hole fauna. Its exquisite glassy umbrella, marked with a cross of yellow or brown by the four radial canals and the gonads, a brilliant row of closely set spots of gleaming phosphorescent green outlining its edge, a fringe of delicate streaming tentacles strung with bead-like clusters of thread cells, are all more or less familiar to many American biologists (Pl. XXXI, fig. 1).

On cloudy days or toward nightfall the medusa is very active, swimming upward to the top of the water and then floating back to the bottom. In swimming it propels itself upward with rhythmic pulsations of the bell-margin, the tentacles shortened and the bell very convex (Pl. XXXI, fig. 2). Upon reaching the surface the creature keels over almost instantly, and floats downward with bell relaxed and inverted and the tentacles extended far out horizontally in a wide snare of stinging threads which carries certain destruction to creatures even larger than the jelly-fish itself (fig.

⁴ AGASSIZ, 1865, p. 125.

1). *Gonionema* continues this fishing, with little respite, all day long in cloudy weather. Occasionally it fastens itself to a blade of eel-grass or some other object near the bottom (Pl. XXXI, fig. 3), or stops midway in its course with tentacles extended, as in my figure (1). In this position it is well-nigh invisible, but a deadly foe to small fish or crustaceans which cross its path.

GONADS.

In the mature *Gonionema* the sexual organs are "frill-like lobes, passing from one side to the other of the chimiferous canal" (Agassiz, 1865). Their form and position are shown in Pl. XXXI, figs. 3, 4 and 5. The free edge of the ribbon of tissue is thickened and rounded, and is bent backward and forward across the radial canal. The color of the gonads has been supposed to afford means of discriminating between the sexes, the males differing from the females in the brighter yellow of the gonadial tissue. But this distinction does not hold, and it is necessary to examine the individual meduse with a lens in order to separate the sexes. The ovarian eggs, enclosed in the ectoderm of the gonads in the female, give them a granular appearance as contrasted with the more homogeneous and translucent tissue of the male. When a large number of the jelly-fish are separated into two vessels, one containing the males and the other the females, the general color tone of the males is brighter and more lively than that of the females, but the specimens in each dish range all the way from light straw color up through orange, ochre, sienna, to dark brown.

EMBRYOLOGY.

It is my purpose to give in outline the main points in the early part of the life-history of *Gonionema*. I have not discovered that this genus exhibits any notable peculiarities in the development of the egg, and I shall therefore lay the greater emphasis upon certain features of the later developmental stages, which have more significance in so far as they are less familiar.

A. Dehiscence.—The eggs are imbedded in the ectodermal tissue of the gonad as in a gelatinous matrix (Pl. XXXI, fig. 5). The round thickened edge of the ribbon contains the riper eggs, but the thinner portion is well packed with maturing ova. Dehiscence takes place by the breaking down of the superficial ectodermal invest-

ment of the gonad and the liberation of the eggs or spermatozoa imbedded in its substance. The contractions of the umbrella in swimming put a strain upon the subumbrellal walls and help to rupture the epithelium of the gonads. What the cytological change is which precedes the extrusion of the sexual elements or the nature of the causes which effect this change are matters of uncertainty. We know only that these conditions can be artificially induced by means to be mentioned presently. The process of dehiscence occupies only a very few moments. Most of the eggs which are ready for fertilization are extruded all at once, coming out of the bell-cavity in a cloud at each contraction of the marginal ring. Two or three minutes after dehiscence begins only a few belated eggs remain to be loosened from the gonads and expelled from the subumbrellal cavity one at a time. Pl. XXXI, fig. 5, is drawn from a sketch of a medusa in the act of spawning. The specimen was held inverted under the microscope in a watch-glass. Although not free to swim it went through the motions, contracting the bell rhythmically. In this way the softened ectodermal tissue of the gonads was ruptured and the eggs expelled. Little round pits are left by the eggs, like bullet-molds.

The earliest date at which fertile medusæ have been found was the first of July; the latest, the last week of September. The period of maximum sexual activity is from the middle of July to the middle of August.

B. Periodicity.—As stated by Murbach (1895), the eggs of *Gonionema* are deposited with great regularity. During the earlier part of the summer dehiscence takes place at about 8 P.M., but later in the season, when dusk comes earlier, the medusæ spawn at 7 or even as early as a quarter past 6. Extrusion of the eggs may be artificially induced. In this respect *Gonionema* differs markedly from some other marine animals which exhibit equal definiteness in the spawning time. Dr. Murbach found that after the medusæ had been shut up in a dark place for an hour, even during the daytime, they would deposit eggs and sperm. My experiments show that this is more likely to be the case in the afternoon than earlier in the day; before 2 o'clock in the afternoon, an hour in the dark would sometimes bring about a deposition of a small number of eggs, and if the period was lengthened to an hour and a half, a slightly larger number of eggs were found in the water.

But after 2 o'clock the hour's shutting away from the light brought about an apparently normal spawning. I found that the withdrawal of light brings about surprisingly definite results. The condition of the tissues arrives at the point requisite for the release of the eggs almost on the minute. This constancy is not appreciably affected by moderate changes in the temperature. A large number of experiments and observations have been made to educe the exact time of stimulation (if we may so speak of an influence which seems to be purely negative) and the results are summarized in the following table. Record was kept of experiments carried on during the whole of the fertile season, partly in one summer, partly in the next. The stimulation-time varies somewhat with the season; the table gives the results obtained during the last week in July, when the eggs were being discharged in the greatest numbers.

Before 2 P.M.	small number	eggs laid after 90 minutes' darkening.
2-3	" almost normal no.	" " " 75 " "
3-4	" fully	" " " 65 " "
4-5	" " " "	" " " 60 " "
5-6	" " " "	" " " 60 " "
6-7	" " " "	" " " 50 " "
At 8	"	eggs laid normally, without artificial darkening.

As the hour approached the normal time for the deposition of the eggs, the precision with which they were discharged became more and more marked. Between 4 and 7 P.M. the time of darkening necessary to produce spawning does not vary more than four minutes on either side of the hour.

Some experiments were tried with a view to inhibiting the normal deposition of eggs, or at least of hindering it, by keeping the eggs in strong artificial light. The results were not conclusive, as the electric lights in the laboratory were not in use until after dusk, when part of the stimulus had already been received. The experiments showed a certain degree of retarding of the process of spawning as a result of the strong illumination. It would be interesting to determine whether the use of stronger light, applied at the commencement of evening dusk, would result in complete inhibition of the process.⁵

⁵ Subsequent experiments show that brilliant illumination has a stupefying effect on medusæ, inhibiting contraction of the bell and almost preventing spawning, though not altogether or in all instances.

It is evident from the above statements that *Gonionema* is exceedingly sensitive to external conditions. Not all cœlenterates are affected in the same degree, and some are apparently not affected at all by changes in illumination. Some medusæ always lay their eggs early in the morning, while others of nearly related genera choose the evening or night. Experiments carried on by Wilson and Donaldson under Prof. Brooks' direction, at Beaufort, N. C., showed that in the case of *Renilla* and some sea anemones, at any rate, changes in light and temperature did not affect the precision with which the regular physiological processes took place. It is well known that a great many marine animals show more or less definiteness in the habit of spawning. Metschnikoff gives a table⁶ showing the time of spawning of a large number of different genera of jelly-fishes. In other groups the same tendency is manifest. This phenomenon is probably the result of the working of natural selection, the habit of laying the eggs at a certain definite time having proved of value to the different species. The fact that in some forms this precision of periodicity is not dependent upon external influences, while in others there is manifest a marked degree of sensitiveness to such stimuli, seems to me to indicate that the tendency has been arrived at by different processes, and may be due to quite different requirements in the various creatures.

But to return to the dehiscence of *Gonionema*: not all the eggs, by any means, which the ovaries contain are liberated at one time. Medusæ have been seen to deposit eggs every night for a week, and while specimens kept in captivity are not very reliable in drawing inferences as to natural processes, this period of sexual activity would, it would seem, be more likely to be shortened than otherwise by the unnatural conditions. After the first three or four days on which spawning took place, a small number of ova were left in the gonads, and on the three successive evenings these were extruded a few at a time. Late in the summer the specimens taken are usually devoid of sexual products, and the gonads small and shriveled.

C. Egg-Envelope.—In freshly laid eggs the polar bodies are only rarely to be found. They are normally given off and lost in the gonads previous to dehiscence. Before fertilization the eggs

⁶ METSCHNIKOFF, 1886, *Embryologische Studien.*

float in a cloud through the water, each one surrounded by a very soft thick gelatinous envelope. If the egg is not fertilized the surrounding mass of semi-fluid jelly slowly shrinks up and the increased specific gravity causes the egg to sink to the bottom. Blister-like vacuoles appear in its substance, puffing out the jelly, and in the course of several days the protoplasm becomes disintegrated and the egg goes to pieces.

When fertilization takes place, the shrinking of the egg-envelope is more immediate and greater in degree, so that the egg sinks at once and sticks to the bottom by means of the viscid substance surrounding it.

Methods.—It may be well to digress at this point in order to mention some of the methods employed in the preparation of material. The adhesive property above referred to is of great assistance in making mounts of the segmenting eggs, as they may be allowed to settle on glass slides, which are afterward run up through all the reagents, without danger of washing off. For sectioning, the best way of securing the eggs was found to be by stirring about in the water with a camel's-hair brush and preventing them from gluing themselves down to the bottom of the dish. They would then stick together in masses, and being protected from too much pressure by the gelatinous covering, they were found to segment normally. The bunches of eggs were large enough to see with the unaided eye, and could be easily transferred to the killing fluid, and afterward stained and cut.

The best reagents that were used for killing were corrosive-acetic, three per cent. glacial-acetic in saturate solution of bichloride of mercury, and the full strength (forty per cent.) solution of formalin. Corrosive-acetic was satisfactory for most purposes, both segmenting eggs and adult medusæ being fixed in this mixture. They were immersed for from one to ten minutes, according to the bulk of the tissues. Pure (forty per cent.) formalin was used very successfully for the younger stages, giving good cytological fixation of segmenting eggs and of larvæ. Fifteen to forty seconds is sufficient to fix the tissues thoroughly. In working with *Gonionema* I have experienced none of the difficulty that seems to be met with in other coelenterates in getting uniform results with formalin material. I have used this reagent, both for fixation and for permanent preservation, with the best results. For narcotizing

the larvæ and adult medusæ, I find menthol crystals the most convenient and rapid chemical to use.

It may be well to mention the method of keeping *Gonionema* alive in the laboratory. Running water is not desirable, and it is of no benefit to either medusæ or larvæ to change the water frequently, as I have learned after much laborious effort to keep the specimens alive in this manner. Balanced aquaria furnish the best environment for these creatures. I succeeded in keeping a large number of larvæ in healthy growing condition for six months in aquarium jars in the laboratory. The quantity of water was kept constant by adding fresh water to make up for the loss by evaporation. Food was furnished in the form of protozoans and other microscopic organisms. Oxidation was secured by means of large quantities of diatoms which were reared for the purpose. Cultures were made from the scrapings of eel-grass, etc., and the diatoms which accumulated from them, collecting in clumps on the bottom of the dish, were scraped into the water with the larvæ. At the end of January, the polyps, which came from eggs laid the preceding August, died without undergoing metamorphosis. Their death was probably due to a lack of food supply sufficient for the requirements of their growing tissues.

D. Segmentation.—The egg is spherical, averaging .07 mm. in diameter. It consists of yellowish, rather cloudy protoplasm, sufficiently transparent to permit one to observe the more conspicuous changes which take place in the substance of the living egg.

Segmentation is total and equal, of the type which is designated by Metschnikoff as "*durschneidende Furchung.*" The cleavage-furrow appears at one side of the egg first and cuts through its substance until it reaches the opposite side, dividing it into two hemispheres (Pl. XXXI, fig. 6). The point at which the furrow starts is that nearest the nucleus, which lies eccentrically in the granular substance of the egg. The first indication of the furrow is a shallow groove, which deepens rapidly and at the same time lengthens so as to embrace the egg meridionally. The furrow is finally completed, superficially, a short time before it has entirely separated the egg into two distinct halves. The last point to be cut off corresponds in position almost exactly with the nucleus, but on the opposite side of the egg. The first cleavage is completed one hour after fertilization. The two daughter-nuclei now lie at

the plane of fission, and at the same distance from the surface of the egg as the original nucleus. The second furrow normally starts on the same point of the surface as the first, and again divides the egg meridionally in a plane at right angles to the first. Sometimes the second furrow starts irregularly, at a point around the egg from the origin of the first furrow. One of the hemispheres is thus divided before the other, as in fig. 7. Fifty minutes elapses between the completion of the first and second furrows. Successive segmentations come in at intervals of forty-five to fifty minutes.

With the eight-cell stage rotation of the blastomeres occurs. The four upper cells turn through an angle of 45° upon the lower ones, so that they come to lie in the valleys between the lower ones, instead of being superimposed upon them. Segmentation continues until a hollow blastula (Pl. XXXI, fig. 8) is produced, a layer of thick cells surrounding a small cleavage cavity. The cells are of uniform thickness, and their outer ends give rise to cilia which drive the egg round and round by their motion within the membrane, sometimes in one direction, sometimes in the opposite.

During this stage the *formation of the endoderm* takes place. The inner ends of the blastomeres are delaminated, the process going on at an equal rate on all sides, until a uniform layer of endoderm cells lies within the ectodermal layer (Pl. XXXI, fig. 9). By increase in size of these endodermal cells the cavity of the egg comes to be entirely obliterated. During the subsequent life-history of the larva no cavity exists within the body until after several marked changes have taken place.

THE PLANULA.

By the rupture of the egg membrane the nearly spherical ciliated larva makes its escape, and starts upon the stage in which it is a swimming planula (Pl. XXXI, fig. 10). Its shape soon changes, becoming narrower and longer at one pole than the other; this narrower pole is to be the future oral extremity of the larva. The cilia serve to propel the planula in a slow rotating progression through the water, usually not far from the bottom. The larger end is directed forward in swimming. The time at which the planula appears is in the morning, about twelve hours after the egg was fertilized. The length of the larva is now between .1 and .15 mm. (Pl. XXXI, fig. 10). This condition persists for a

varying time. Toward the end of this time the first indications of a *coelenteric cavity* appear in the arrangement of the cells at the posterior end of the swimming larva (Pl. XXXI, fig. 11, *P*). Their inner margins come to lie in a straight line, following the long axis of the larva (Pl. XXXI, fig. 11, *C*). This process is better understood when we notice that in changing its shape from the spherical morula to the elongated planula the larva also underwent a slight rearrangement of its cells. The endoderm was first formed as a spherical mass, and its cells were all conical, radiating from the centre to the surface. But as elongation took place in the formation of the planula, the cells were stretched out into a cylinder and their inner ends overlapped irregularly, as is shown at the anterior end (*A*) of fig. 11. When the coelenteron begins to be developed, the inner ends of these upper endodermal cells change their position somewhat and, as above stated, meet along a continuous line. At the same time a change is to be noticed in the cells at the surface of the oral pole. The cell walls at this point become less distinct (Pl. XXXI, fig. 11, *O*), and finally a disintegration of the boundaries leaves the tissue an undifferentiated layer of protoplasm. Before separation of the tissue to form the definitive coelenteric cavity, the larva stops swimming, loses its cilia, and settles down upon the bottom. The larger end, which was directed forward in swimming, is downward. Between the free-swimming stage and the sessile hydra-stage there frequently, though not always, intervenes a condition which reminds one of a minute planarian in its shape and movements. The planula settles down upon the bottom and slowly glides along by a rhythmic wave-like progression. This condition seems to take the place of the last part of the ordinary and evidently more normal free-swimming stage, and is perhaps due to the unfavorable conditions of the laboratory. This condition is not at all like the pathological plasmodial forms to be mentioned below. Its changes in shape are slight, and its manner of movement rather a glide than a protoplasmic flowing. None of the definiteness of structure is lost, and these larvæ transform into hydras as soon as those which change directly from the free-swimming planulae. It is, then, not a phenomenon of degeneration, nor, on the other hand, an essential phase in the life of the animal, but rather an intermediate and probably accidental condition.

THE HYDRA.

As soon as the planula-stage has given place to the settled hydra-stage the coelenteron becomes complete. The mouth appears at the free end where the tissue has previously showed indications of disintegration, at the end of the axial line formed by the endodermal cells. At first the mouth is visible only when the specimens are killed and cleared or sectioned. Soon, however, it becomes large enough to see in the live animal by focussing down from above with a high-power lens. It then appears as a minute pit in the ectoderm. The coelenteron is more distinct at the upper end than below, where it disappears into the loosely constituted cell-mass of the interior. The definite cavity of the coelenteron is somewhat later in making its appearance. When finally established it is lined with a thick layer of columnar endodermal epithelium. At its bottom it flares out in following the contour of the body-wall, as it appears in Pl. XXXII, fig. 15, which shows a late stage, but the same condition of the coelenteron as exists in the newly transformed larva. The figure also shows a thickened core of endoderm which projects upward into the coelenteron as a *gastric peduncle*. This conical mass of cells develops during the latter part of the hydra-stage.

A. Tentacles.—In the later transformation of the developing *Gonionema* no definitely determinate periods separate the times of active change. The development time is variable, depending upon external conditions of food, temperature, etc. In an average larva, however, the first tentacles make their appearance during the third week after the fertilization of the egg, or a week after the larva becomes attached. Two tentacles appear opposite one another at a level about one-quarter of the distance from the upper pole of the hydra (Pl. XXXII, fig. 12). They are knob-like when they appear, but grow rapidly to a considerable length, the few endodermal cells which form the core of each tentacle increasing in number. Fig. 12 shows a vertical section of a two-tentacled polyp of the fifth week. The manner of origin of the tentacles will be described in the section on the origin of tentacles under "The Medusa."

The second pair of tentacles (Pl. XXXII, fig. 14) appear soon after the first, and by their rapid growth soon become as large as the first pair, from which they are then no longer distinguishable.

Irregularities are common in the appearance of the tentacles of the polyp, as in the adult. It frequently happens that only one of the second pair ever makes its appearance. Or one may be slow in arising, and always remain smaller than the other. On the other hand, an abnormally large number are frequently developed, individuals with five or six being not uncommonly found (Pl. XXXII, fig. 13).

B. Form of Cœlenteron.—The appearance of the tentacles is accompanied by alterations in the form of the cœlenteric cavity. The rapid growth of the cells at the points where the tentacles arise and the outpushing of the tissue in the process seem to affect the contour of the body-wall

over a considerable area, so that diverticula of the cœlenteron and of the mouth extend in the direction of each of the tentacles. A stellate arrangement results, the mouth being in the form of a cross. This corresponds exactly with the condition in the medusa, especially in young specimens (Pl. XXXIII, fig. 19), in which the twisting which in older individuals obscures somewhat the true relation of parts has not yet taken place. In the three-

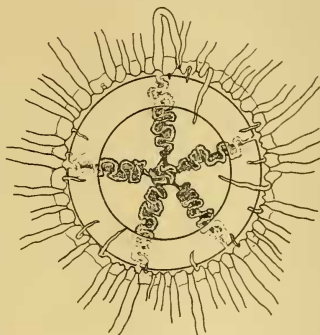


Fig. 1.

Abnormal five-parted medusa, showing agreement in plan between oral lobes and radial canals.

or five-tentacled hydra the number and arrangement of the oral lobes corresponds with the number and arrangement of the tentacles. Fig. 13, Pl. XXXII, represents a polyp with five radial parts, in which one lobe of the mouth is bifurcated. This condition is very similar to that frequently met with in adult medusæ (text fig. 1). The whole aspect of the hypostome of the *Gonionema* polyp is very similar to that of the manubrium of the young medusa. The ectoderm at the edges of the mouth becomes thickened and armed with nematocysts, which have by this time made their appearance, in a manner to be described later, over a large part of

the body of the hydra. Below the mouth the hypostome becomes narrow and tubular and distinct from the rest of the body, a decided angle separating them at the level of the tentacles.

HABITS.

One of the most striking habits of the adult jelly-fish is its prehensile propensity. The adhesive organ at the "knee" of the tentacle is composed of long slender glandular cells, packed into a thick cushion which is inclosed within a strongly muscular rim or collar (Pl. XXXIII, fig. 20). This organ is located on the aboral side of the tentacle. When at rest the jelly-fish lies on the bottom with inverted bell, the tentacles widely extended horizontally and attached to the bottom by means of the combined cement gland and vacuum cup near the tip (Pl. XXXI, fig. 3). How this habit of inverting itself could have come to be acquired primarily by the adult medusa it is hard to see. But if, as I shall give my reasons for believing, the medusa arises by direct metamorphosis from the hydra, the habits of the hydra would naturally be more or less permanent in the adult. It may be that this particular habit is more likely to be first acquired by the larva than by the adult. The tentacles of the hydra reach a relative length greater than in the case of any other known hydroid polyp. They frequently stretch out in the water for a distance three or four times the height of the polyp. Fig. 14, Pl. XXXII, shows a hydra with the tentacles fully extended, their tips touching the ground in the characteristic attitude. The drooping of the tentacles is evidently caused by their extraordinary length, and is almost as unusual an occurrence among the hydromedusæ. At the points where the tips of the tentacles come in contact with the bottom they spread out somewhat, forming a sole-like surface which is closely applied to whatever object the polyp is settled upon (Pl. XXXII, fig. 14). This smearing out of the tentacle tips is like that which occurs in live specimens of hydra held between slide and cover-glass for examination. Both polyp and medusa remain when at rest with the mouth expanded, the manubrium stretching upward, the tentacles widely extended and drooping to the bottom. When an animal swims against one of the tentacles, the reactions are much the same in the polyp as in the adult. The feeding habits of *Gonionema* have been described at

length by Yerkes.⁷ His account would apply almost as well to the process in the hydra. The tentacle which comes in contact with the prey is contracted with a suddenness and vigor which belies the apparent inertia of the moment before. The victim is seen to be firmly spitted on the microscopic lances of the nematocysts, and it is evident that the first thing that happened when the animal touched the tentacle was the discharge of all the thread cells in that region. The tentacle in contracting carries the food, protozoan or minute worm, or whatever, toward the mouth. The long manubrium then moves about slightly as if in search of the morsel. Finally the tentacle places the food directly upon the mouth (Pl. XXXII, fig. 16), which proceeds to turn itself over the object and work it downward until it vanishes into the gastric pouch of the polyp.

DEGENERATION PHENOMENA.⁸

For some reason or other, not understood at present, the larvæ in one of my aquarium jars began when three months old to exhibit most singular forms and activities. All appearance of the hydra form was lost, ectoderm and endoderm becoming indistinguishable and cell outlines dissolved. The larva in this condition had very much the appearance of an amœba. The specimens slumped down on the bottom of the aquarium in a shapeless mass, and by protoplasmic flowing changed their shape through an endless variety of forms, moving slowly from point to point. Thin pseudopodia were sent out, along which the substance of the organism flowed, and by the breaking of the connecting isthmus divided into two. The fragments became smaller and smaller until no longer recognizable. These abnormal larvæ remained alive for six weeks, after which no trace of them was to be seen.

BUDDING IN THE LARVÆ—METAGENESIS.⁹

Contrary to Haeckel's statement that in the group of jelly-fish which he calls the "Trachomedusæ" metagenesis does not occur, in

⁷ R. M. YERKES, "The Sensory Reactions of *Gonionemus*," *Am. Journ. Physiology*, February, 1902.

⁸ More fully described in the *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, August, 1902.

⁹ An earlier draft of this section appeared in the *Johns Hopkins University Circulars*, June, 1902.

Gonionema, which falls into that group, this process does take place. By a form of non-sexual multiplication different from any which has previously been described for any member of the hydromedusæ, an intermediate process of reproduction is introduced into the life-history of *Gonionema*, whereby a large number of adults are produced from a single egg. Asexual multiplication in the larvæ of Scyphomedusæ has been known since 1841, when Sars saw and described the formation of buds in a scyphistoma of uncertain identity, but probably either an *Aurelia* or a *Cyanea*. Since that time several analogous cases have been made known. The scyphistoma larvæ of *Cassiopea*, for example, were found producing eggs in large numbers by Bigelow (1900), who gives a detailed account of the method of budding in a monograph on this Rhizostome. It may be further stated that in general the non-sexual process of production of buds by the larvæ is an important method of multiplication among the Discomedusæ. The buds usually develop, after detachment from the parent polyp, into a second generation of scyphistomas, identical in form and fate with the original ones. Buds may arise on the body of the scyphistoma, or upon stolons from its base, and either singly or several at a time. In *Cotylorhiza* the buds develop so rapidly and remain attached so long that large clusters accumulate about the base of the scyphistoma. According to some authors, Goette for example, the distal end' of the bud in *Aurelia* and *Cyanea* is destined to become the oral end of the detached larva, developing mouth and tentacles. Friedemann, on the other hand, says¹⁰ that in *Aurelia* he has found the opposite condition, the mouth being invariably developed at the *attached* end of the bud. This is the common relation in other forms.

In *Cunina*, which falls into Haeckel's order the "Narcomedusæ," the ciliated tentacled larva multiplies by buds produced from an aboral stolon. These buds are not detached until mouth, digestive cavity and tentacles are well developed. Several are produced simultaneously, and are attached to the parent by the oral extremity. The description of this remarkable process is given by Prof. W. K. Brooks in *The Life-History of the Hydromedusæ* (1886).

¹⁰ Postembryonal Entw. von *Aurelia aurita*, *Zeitsch. f. w. Zoologie*, LXXI, 2, 1902.

It is my purpose in this section to give an account of a process of budding in a medusa very different from *Cunina*, one in which the asexual multiplication takes place very differently. In *Gonionema* the buds are produced in a manner which reminds one very strongly of the similar process in *Cassiopea*.

In the course of my general study of the development of *Gonionema* I came upon the budding larva (text figs. 2-10). From a lot of eggs obtained at Woods Hole, in August, 1901, a large number of polyps developed and were kept alive in a balanced aquarium for several months. This lot was left at Woods Hole in as nearly natural conditions as possible until the last of November. The water was kept fresh by frequently renewed supplies of diatoms and ulva, and occasionally changed by carefully adding a quantity taken from the natural habitat of the medusa in the eel-

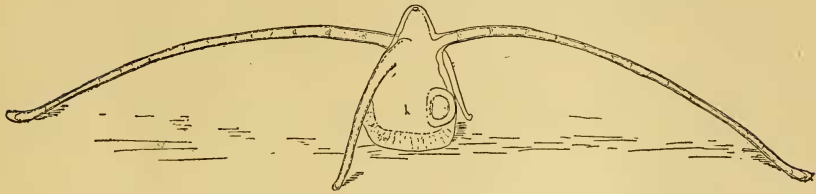


Fig. 2.

Five months old polyp with bud just forming.

pond. A low temperature was maintained. When these larvæ were received from Woods Hole (November 28) they were apparently thriving well. They had all settled upon the Minot watch-glasses which had been placed in the bottoms of the dishes. These were easily removed without disturbing their contents. The watch-glasses were numbered and the positions of the polyps carefully noted and mapped. Successive examinations showed that the number of polyps was increasing, and on December 3 it was seen that one or two of the largest specimens had rounded knob-like bodies upon them; these were at once recognized as buds. The specimens were examined as frequently as it was thought safe to remove them from the jar, and camera drawings were made of the growing buds. Observations were made of the different stages in the development of fourteen buds; their phases agreed in all the main particulars.

The first indication of the appearance of a bud upon any individual polyp was a rounded eminence upon the hydrocaulus (fig. 2). It was usually located at a level about half-way between the base of the polyp and the ring of tentacles, as in the figure, and interradially—*i. e.*, at the end of a radius which bisects the angle between two tentacles (fig. 6). Never more than a single bud appeared at one time upon any polyp.

All three body-layers—ectoderm, endoderm and mesoglaea—of the parent are involved in the formation of the bud. The cells of both ectoderm and endoderm multiply rapidly in the region of the wall of the polyp where the bud is about to be formed. The endoderm pushes out as a rounded protuberance, covered by the ectoderm in a layer of constant thickness (fig. 3). A

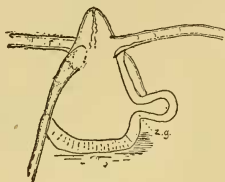


Fig. 3.
Same bud eight hours old.

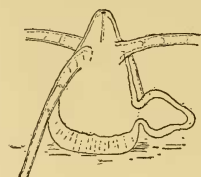


Fig. 4.
Bud one day old.

thin supporting lamella of mesoglaea lies between the two. As the bud increases in size it bulges out at its base, around the stalk which connects it with the polyp, and it also develops rapidly at the tip of the free end. In this way it becomes pear-shaped (fig. 4). As the drawings indicate, the ectoderm is of the same thickness in the bud as in the parent (fig. 3). Indeed, so nicely regulated is the rate of growth of the two tissue-layers that the thickness of the ectoderm does not change appreciably during the entire growth of the bud, previous to its detachment. The cells of the endoderm are irregular, loosely constituted and coarsely granular, and their walls are hardly discernible. No cavity exists in the bud until considerably later. The endoderm of the bud now becomes separated from that of the parent, by the constriction of the ectoderm and the cutting off of the core of endoderm which filled it. Its appearance is as represented in fig. 5, an isthmus of clear elastic ectodermal tissue uniting the bud to the parent. By rapid

centrifugal growth the bud becomes sausage-shaped, and as long as the diameter of the polyp (fig. 6). Soon after the bud reaches the stage shown in this figure, it becomes detached from the polyp.

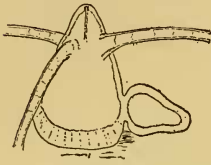


Fig. 5.

Bud three days old. Endoderm isolated from that of parent by constriction of ectoderm.

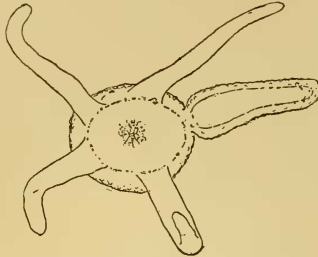


Fig. 6.

Bud four days old. Ready for detachment. Showing interradiial position.

In only one instance was I so fortunate as to see this process taking place. In this individual the bud was drawn out into a long finger-like body, its distal end drooping almost to the ground. Soon the ectodermal isthmus began to stretch out and dwindle in diameter, until it was merely a thin stem of transparent protoplasm (fig. 7). The bud seemed to be reaching out and trying to free

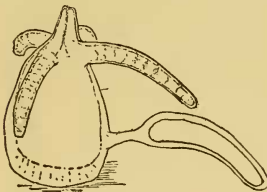


Fig. 7.

Another individual. Bud in process of detachment, showing elongated ectodermal isthmus.

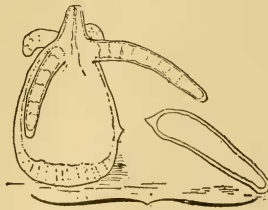


Fig. 8

Same bud fifteen minutes later. Bud settling down on distal end.

itself from the limitations of its connection with the parent. This stretching of the isthmus was brought about by constriction of the tubular ectoderm, as by circular muscle fibres. When this stretch-

ing had gone on until the isthmus was a quarter as long as the entire bud (fig. 7), it began to grow still thinner at its middle, and finally, just half an hour after it first began to stretch out, it broke in two and the bud fell away from the parent (fig. 8). The two ends of the connecting stalk shrank back into the tissues of the bud and of the parent, appearing for a time as minute points of protoplasm, as in the drawing. After separation from the polyp this particular bud settled down at once upon the previously free or distal end, and began an independent existence (fig. 9). Other



Fig. 9.

Detached larva, just settled down, three days after detachment.

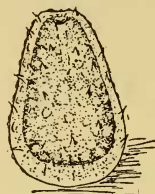


Fig. 10.

The same four days later. Basal ectoderm thickened.

observations, however, indicate that the usual course of development is slightly at variance with this instance, and that it includes a motile period of from three to four days, intervening between the detachment of the bud and its settling down as a hydra. A bud which was growing upon the body-wall one day would be gone the next, and for some time could not be found. Then it would suddenly appear in some previously vacant spot, at a distance from the polyp, perhaps in an entirely different watch-glass on the bottom of the aquarium, with its tentacles just beginning to appear. In one case the bud was drawn and measured when it seemed to have reached its full size and to be ready to drop off. This was done one evening, and the next morning no bud was to be seen upon the parent polyp. Three days afterward a small polyp was found upon a spot which certainly had been unoccupied up to that time, according to diagrams made at short intervals. This was a larva like that in fig. 10. It was measured, and

although somewhat different in shape, as nearly as one could estimate its bulk, it corresponded exactly with the bud which had disappeared. Similar observations were so numerous that it seems unavoidable to consider the motile form a normal phase in the non-sexual as in the sexual process of multiplication. The precise nature of this intermediate condition is not yet determined. It seems probable that it is a creeping unciliated form, although my first conjecture, that it was a ciliated planula, has not yet been proven erroneous.¹¹ This peculiar phase is an interesting case of reversion in the non-sexually developed larva to a condition earlier, in point of ontogenetic order, than that of the parent at the time of budding.

The subsequent history of the bud has been definitely followed. After settling down upon the bottom it repeats the changes which occur in the sexually produced polyp. The newly arisen larva (fig. 9) loses its planula shape, becoming shorter and thicker, especially at the base, on account of the plastic character of the tissues (fig. 10). It has now secured a firm hold upon the bottom, being so closely applied that it is quite hard to dislodge it. The cells at the base increase in thickness until they form a columnar epithelium. After the first day a slight pit indicates the point at which the coelenteron is to open externally. This process, as observed in a number of cases, is exactly the same as in the sexually produced polyp. The tentacles also make their appearance in the same manner as described for the hydra which developed from the egg.

The length of time required for the complete development of a bud, from its first appearance on the hydrocaulus of the parent as a simple knob until the completion of the formation of the coelenteron and the appearance of the tentacles, is from ten to fourteen days: (a) the first period, including as far as the detachment of the bud, 5 days; (b) motile form, 2 to 4 days; (c) from attachment to appearance of tentacles, 3 to 5 days. These periods refer, of course, to specimens in captivity.

Pl. XXXII, fig. 17, shows a specimen from an entirely different lot of polyps from those which exhibited the budding phenomena shown in the text figures. This polyp was killed when 23 days old. It may not be a normal individual, but as it shows a tendency to divide transversely it seems worth while to call attention to it. The

¹¹ PERKINS, *loc. cit.*

coelenteron has completely divided into two, and the endodermal wall of the pouch has grown in as a solid partition between the two new pouches. The aboral portion of the body, or hydrocaulus, is seen to be considerably longer than is usually the case. It is interesting to compare, in this connection, Dr. Murbach's account¹² of the transverse fission of *Hypolytus*.

TRANSFORMATION OF THE POLYP.

Up to the present time all efforts to secure specimens of the larval *Gonionema* in their natural habitat have been well-nigh fruitless. Although the eggs are laid in enormous numbers during four to six weeks of the summer, and even when kept in the laboratory a large proportion develop, it has yet been impossible to find the polyps in the eel-pond where the medusæ are so plentiful. Many speculations have been hazarded as to the condition in which the larvæ pass the cold months of winter, and no small energy and time have been expended in attempting to get at the secret. And yet I am much more ready to believe that the difficulty has been with our methods of search than that any extraordinary transformation in form or change in habitat should render the success of such search impossible. This seems the more likely from the fact that during the summer when the medusæ are laying their eggs most plentifully, and within a few days after an egg is laid it has developed into a fixed polyp with tentacles, the extreme minuteness of size and transparency of substance of the polyps hide them completely; and yet they must be present in great numbers on the stones and in the mud at the bottom of the eel-pond. Very few specimens have been found, although careful search has been made by others than myself. It is quite out of the question to suppose that the larvæ which develop into the medusæ appearing each year in great numbers in the eel-pond, have undergone their transformation in deep water, having been swept out to sea from their birthplace. In such case the adults would appear in much wider range of habitat—in some of the bays and inlets of the coast where the conditions seem almost the same as in the eel-pond. The fact is that only a few stragglers are ever found in the vicinity, not

¹² L. MURBACH, "Hydroids from Wood's Hole," *Quarterly Journal*, Vol. XLII, Pt. 3.

more than would be swept out of the shallow water by the tide. Not only these considerations, but all the other indications seem to point to a direct transformation of the polyp to the adult gonosome without leaving the eel-pond. The habit of the polyp of resting with tentacles extended and adhering to the bottom, the feeding reactions, the form of cœlenteron, manubrium and oral opening, the manner of origin of the tentacles, all resemble the corresponding conditions in the adult so closely that it is easy to regard this as the most likely theory. May it not be that the same type of metamorphosis as that which takes place in *Liriope* (Brooks, 1895) is passed through in this genus as well? In *Liriope* the cœlenteron is transformed into the system of chimiferous tubules by the growth of fusion areas which unite the upper and lower walls of the cavity, except where they are to be left separate along the lines of the canals. Pl. XXXII, fig. 18, is a camera drawing of a twelve-tentacled gonosome of *Gonionema*, which has very much the appearance of the newly metamorphosed *Liriope*.¹³ The transformations which are necessary to bring about the adult from the larval form are a change in the cœlenteron to a system of tubes; the centralizing of the diffuse nervous system to form the two nerve-rings; the appearance of new tentacles provided with adhesive disks, and of tentacles modified to the form of sense-organs, from the expanded tentacular ring; and the growth of the velum. The relative size of the fully developed polyp and the youngest medusa offers no contradiction to such a conception of direct metamorphosis; if the polyp grows as rapidly in the natural environment of the eel-pond as in the laboratory, even allowing for a long period of absolute quiescence during the cold weather, the discrepancy in size is easily accounted for.

YOUNGEST MEDUSÆ.—ARRANGEMENT OF TENTACLES AND
SENSE-ORGANS.

During the last of June, 1900, a number of very small specimens of *Gonionema* were taken in a tow net at the surface of the eel-pond. Several of these had sixteen tentacles, some had twelve, one had only eight. A careful study of these very young and evidently recently metamorphosed gonosomes has brought out some exceedingly interesting points.

¹³ BROOKS, 1895, Pl. 41; HÆCKEL, *Die Russelquallen*, Pl. 12.

Hargitt, in his paper, *Variations Among Hydromedusæ*, discusses the arrangement of tentacles in *Gonionema*. He approaches the question as a student of variations, and unfortunately lacks the young material from which I have found it possible to educe very definite rules in the arrangement of marginal organs and their order of appearance. As a natural result Hargitt comes to the conclusion that so much irregularity occurs as to render it impossible to discover any definite order of appearance or ultimate arrangement in these organs. It is true that the abnormal specimens which he studied most closely do show very little regularity, as would indeed be expected. But in normal individuals quite a remarkable degree of precision is manifest in the position and order of appearance of tentacles and sense-organs, with reference to each other and with reference also to previously arisen organs of the same kind. This is particularly true in the younger stages.

If we examine the eight-tentacled medusa the following points are noticeable: First, the tentacles are evidently of two cycles, in order of appearance. The four at the ends of the radial canals, or the *perradials*, are equal in size, and larger than the four *interradials*, which are also of equal size. These tentacles are very similar in appearance and structure to the larval tentacles, and there seems little reason why the larger perradials may not be the permanent larval tentacles.¹⁴

Second, the sense-organs are four in number and placed in definite positions, relative to the tentacles. If we look at the bell-margin from the oral side, the newly arisen tentacles in the four quadrants have apparently crowded in between the sense-organ and the perradial tentacle, which comes before it as the hands of a watch go. Fig. 11 shows this stage, and is made from a camera drawing of the eight-tentacled medusa. The relation which is here exhibited in the youngest stage of the free-swimming gonosome is the same throughout the growth of the medusa: *wherever a rudimentary or newly arisen tentacle lies on the bell-margin, it will always, normally, be found to lie just in front of a newly arisen sense-organ, and just after a larger tentacle, i.e., one of an earlier cycle.*

Much has been written to show that coelenterates, and especially

¹⁴ This conclusion is strengthened by work done since this paper was written.

members of the hydrozoa, show bilateral symmetry, either in the normal condition or when they depart from the normal form and may be supposed to revert to a more primitive type (Mayer, 1901, *e.g.*). *Gonionema* shows a very different plan from that of bilateral symmetry. It is rather a certain sort of radial symmetry which has nothing bilateral about it—one in which the radial parts correspond exactly to each other, and are superimposable, but none of which is the reflected image of any other. I shall call this relation one of *cyclic symmetry*. With reference to the order of appearance of the marginal organs I shall speak of *cyclic sequence*.

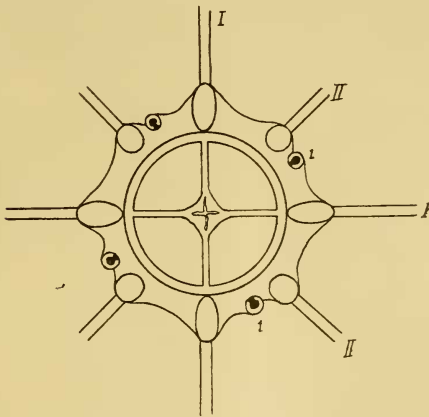


Fig. 11.

These terms were suggested by Prof. Morley, of the mathematical department of Johns Hopkins University.

New tentacles make their appearance four at a time, or, so to speak, in quartets; they are 90° apart, so that they occupy identical positions in the four quadrants of the marginal ring. But while the tentacles, and the sense-organs as well, appear to rise in fours, the condition in the larva, and in frequent instances among the adults, indicates that a paired origin is more primitive and fundamental. It is the rule in the early larvæ that two tentacles appear opposite to one another (Pl. XXXII, fig. 12), and later

the second pair of the quartette. It often happens that in the adult medusa two members of a quartette, in opposite quadrants, are retarded in making their appearance. In *Aurelia* Claus established the theory that while the larval tentacles seem to come in fours after the earliest stage, the first four tentacles appear first two, then two more, as is the case in *Gonionema* (v. Claus, 1892). Goette (1887) has examined a great number of specimens of the younger stages of *Aurelia*, and has come to the same general conclusion as Claus with regard to the primitive paired condition and the significance of this in the philogeny. Haeckel (1881), however, regards the appearance of two tentacles in advance of the second two as an accidental and insignificant occurrence; he takes four for the primary number. While this tendency to a paired origin of the tentacles disappears after the earliest stages in *Aurelia*, *Gonionema* exhibits this tendency in frequent instances during the whole life of the animal. Its occurrence in the appearance of the sense-organs is of the same significance, because, as will be pointed out below, these organs are modified tentacles. Pl. XXXIII, fig. 19, shows this condition in the sense-organs, quadrants *A* and *C* having five, while in quadrants *B* and *D* only four are developed. It is true that other variations than these do occur in the appearance of the tentacles and sense-organs in the adult, and of the tentacles of the larva. Polyps with three, five or six tentacles are not uncommon (Pl. XXXII, fig. 13). It is noticeable that departures from the normal number correspond very closely in polyps and adults. This would be expected from the evidence that the larval tentacles are permanent, and that they determine the position of the four radial canals in the normal medusa, or of the three, five or six in aberrant specimens. This inference seems a likely one from the fact that in the adult medusæ the tentacles which, from their larger size, are presumably of the first cycle are always, normally, located at the ends of the radial canals. The inference is that five-parted medusæ were five-tentacled polyps. This is borne out by comparison of the relative numbers of each kind of variation among medusæ and among polyps. Hargitt (1901) has tabulated the number of medusæ that have come under his notice having three, five and six radial canals; and he finds that about five per cent. are irregular in this regard, *i.e.*, vary from the normal four-parted condition.

While I have not had a great number of specimens of the polyps from which to compute averages, my counts show quite a striking similarity to those which are given by Dr. Hargitt for the adults.

Among all the varieties of geometrical figures which appear in the arrangement of parts among the various orders of cœlenterates, there is none, so far as I can find, which is at all comparable with that which appears in the arrangement of tentacles and sense-organs in *Gonionema*. The only suggestion of such a plan of arrangement as this is given in a paper on the later development of *Aurelia*, by Friedemann (1902). In the course of the paper this author describes the origin of the eight tentacles which follow the first eight. Four of these appear at once, the other four later. In the appearance of the first four, two possibilities arise, according to Friedemann. Either the four arise in bilaterally symmetrical

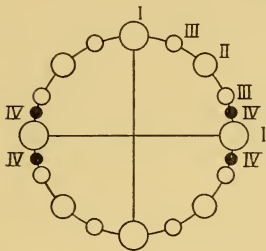


Fig. 12.

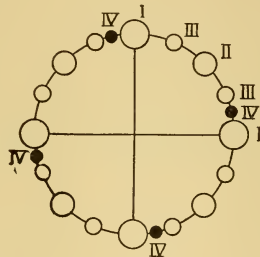


Fig. 13.

positions in the four quadrants, the two halves of the tentacle-ring being reflected images one of the other, and the new tentacles appearing one on either side of the two opposite perradial tentacles (fig. 12); or else they appear in identical positions in the four quadrants, one appearing next in front of each perradial tentacle, as the hands of a watch move (fig. 13). Friedemann's figures do not make it clear that he actually found specimens in exactly this stage. It appears more probable that he interpreted older stages by this theory. But it may easily be true that in other groups than that to which *Gonionema* belongs the tentacles originate according to a plan of cyclic symmetry, or that such a condition sometimes appears, irregularly, as may be the case in *Aurelia*. In *Gonionema* the rule holds with remarkable constancy.

From a study of successive stages of growing medusæ the following table is compiled to show the relation in time of appearance of tentacles and sense-organs. The numbers in brackets in the column of sense-organs indicate half-quartettes, the corresponding pair in each case having been delayed in appearance. Since the sense-organs are only half as numerous as the tentacles, they appear with half the rapidity, and are therefore more frequently found in

	TENTACLES.		SENSE-ORGANS.
Larval	2	(2)
	4	4
	8	(6)
	12	8
	16	(10)
	20	12
	24	(14)
	28	16
Adult	32	(18)
	36	20
	40	(22)
	44	24
	48	

this condition of incomplete quartettes. That is, if a jelly-fish were killed when the tentacles and sense-organs were in the precise stage indicated by the line *a b*, for instance, the fifth quartette of sense-organs would be found only half formed—five sense-organs appearing in two opposite quadrants, and only four in the other two. This is just the condition which exists in the specimen shown in Pl. XXXII, fig. 19. The numbers indicating the sense-organs are put at the intervals between those indicating tentacles, to show that while the eight tentacles between the eight-tentacled and the sixteen-tentacled stages, for instance, are appearing, the four sense-organs which make up the second quadrant are appearing.

Another rule is followed by the marginal organs in their order of

appearance. Each new tentacle arises not only just in front of a sense-organ, but in a definite relation to the older tentacles. And the same thing is true for the sense-organs. It is therefore possible,

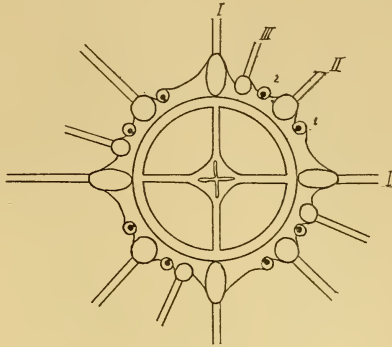


Fig. 14.

from a study of successive stages, to predict where each new quartette of tentacles or sense-organs will arise. The diagrams shown

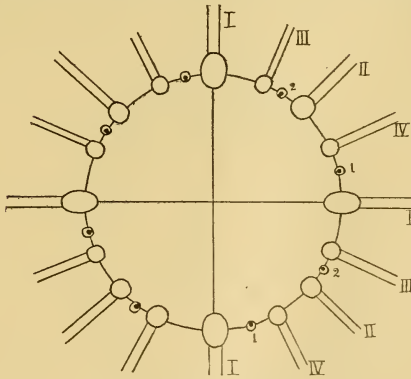


Fig. 15.

in the text-figures are from camera drawings of mounted whole medusæ. If we examine text-figure 14 we see that T. (tentacle)

III follows T. I; and text-figure 15 shows T. IV following T. II.

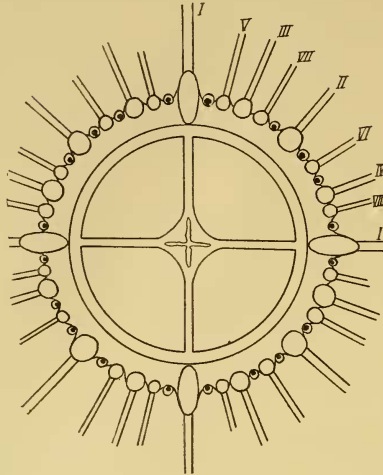


Fig. 16.

Thus T. III and T. IV form a series, arising in corresponding

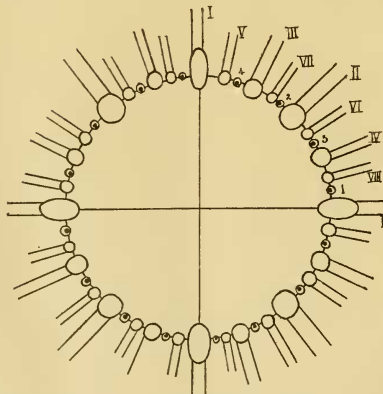


Fig. 17.

positions in the quadrant relative to the tentacles already present.¹⁵
The next series consists of four tentacles in each quadrant, T.V.

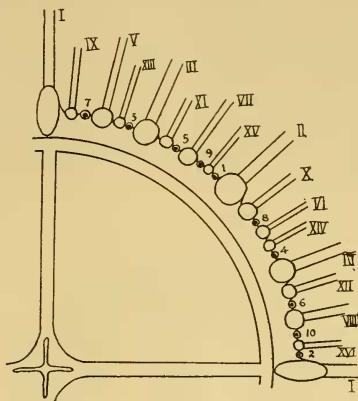


Fig. 18.

to T. VIII. This brings us to the thirty-two-tentacled stage (text-figures 16 and 17). In this it will be seen that T. V follows T. I,

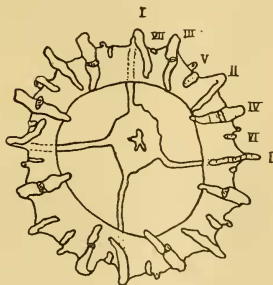


Fig. 19.

T. VI follows T. II, T. VII follows T. III, T. VIII follows T. IV, *i.e.*, four numbers intervening in each case. The next

¹⁵By "series" is not meant "cycle," with the idea of simultaneous appearance; the notion is one of relative position simply.

series comprises T. IX to T. XVI, which follow the same plan in order of appearance, T. IX following T. I, etc., eight numbers intervening in each case (fig. 18).

While this may seem more like a fanciful exercise of the imagination than an actual condition in nature, the truth is that the larger the number of specimens in which one tests the arrangement of the marginal organs by this rule, the more will one be convinced of the remarkably constant adherence to it. Given a specimen with, say, twenty-eight tentacles, such as that represented in fig. 19—this is a drawing of a specimen of *Olindias* from the Bahamas, a

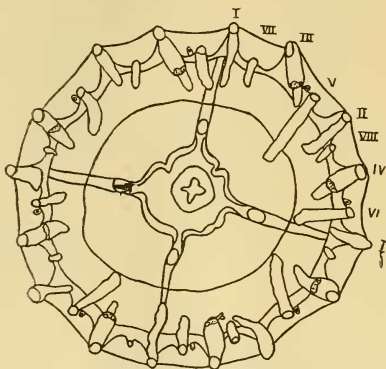


Fig. 20.

genus which follows the same rule in the order of appearance of the tentacles as *Gonionema*—the sense-organs are not so numerous in *Olindias*. In this specimen the most recently arisen tentacle in each quadrant is evidently the one numbered VII, lying just after each perradial tentacle. Then, if the rule which we have deduced applies in this case, we should expect to find the eighth tentacle in each quadrant arising in a corresponding position with relation to the interradial tentacle.

And such we find to be the case. Fig. 20 shows a slightly older specimen of the same species in which we plainly see the eighth tentacle in each quadrant lying in its appointed place (VIII).

It would be singular indeed if there were no exceptions at all to this general rule. Many variations from the regular cyclic symmetry do occur, but only as many as would be expected from the marked tendency to variability in all parts of the medusa. These variations no more obscure the normal definiteness of plan than the occurrence of six or seven-rayed star-fish obscure the normal pentamerous form in echinoderms. Text-figure 21 shows an irregular condition, the fourth tentacle in each quadrant having arisen aberrantly, following instead of preceding the first sense-organ (1).

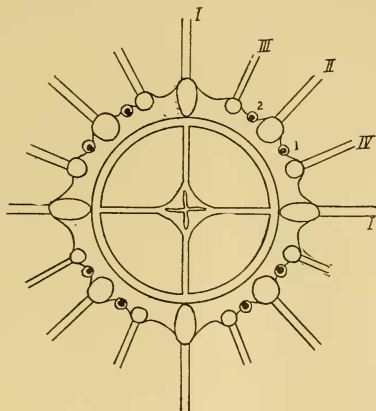


Fig. 21.

In Pl. XXXIII, fig. 19, one of the latest arisen quartette had not put in its appearance (see arrow in quadrant A). In the older specimens, the number of irregularities increases. It seems to me that the bell-margin increases in extent subsequent to and as a consequence of the increase in the number of tentacles, rather than that the tentacles arise, haphazard, wherever there is space enough on the margin to accommodate them (Hargitt, 1901). Certain it is that the most crowded part of the bell-margin at any particular moment is that from which new tentacles are in the process of arising.

HISTOGENESIS OF MARGINAL ORGANS.

A.—In the larva.—The similarity in the appearance of the tentacle-rudiment in polyp and in gonosome make it desirable to describe both in the same connection. The account of the origin of the tentacles in the polyp was therefore reserved for this section. At first the larval tentacle is merely a small round knob, externally, and internally it is made up of a core of two or three endodermal cells. When the tentacles make their appearance the body wall of the polyp is made up of the double layer of cells, the ectoderm and endoderm, separated by the thin supporting lamella of mesogloea. These three layers are pushed out somewhat in the growth of the tentacle, the region of greatest activity being the endodermal layer, where the core of the tentacle is formed by a rapid out-growth of the cells of the body wall, accompanied by multiplication of these same cells. After some weeks the cavity of the coelenteron becomes drawn out in a diverticulum in the direction of the axis of the tentacle, so that the upper part of the gastric cavity becomes stellate in cross section. Pl. XXXII, fig. 15, shows this condition in a five-months'-old polyp. This cavity does not reach out into the tentacle itself in any of the specimens which I studied, but may do so before metamorphosis takes place. During the whole of larval life, the tentacle is made up of a core of endodermal cells in a single row, as is the case in hydra. Fig. 11 shows the first pair of tentacles only developed, and the cell-layers are seen as described. The endoderm cells are filled with a loose protoplasmic mass (Pl. XXXIV, fig. 24, *End.*) and the nucleus is conspicuous. The condition which is seen in an adult tentacle with several cells of endoderm surrounding the central cavity (fig. 23) is easily derivable from the larval condition by longitudinal fission of the endodermal cells, repeated until a cross-section of a tentacle cuts several cells (Pl. XXXIV, fig. 25).

B.—In the Adult.—The regularity with which the tentacles and sense-organs make their appearance in the adult, as previously described, makes it possible to locate with comparative certainty the beginning of one of these organs upon the bell-margin. Pl. XXXIV, fig. 24, is from a section of a medusa, cut horizontally at the point of origin of one of the tentacles. The figure shows the aspect at the level of the tentacle, somewhat above the velum.

Both cell-layers are seen to be concerned in the formation of the new tentacle. The endoderm (*End.*) is pushed out from the region of the circular canal, and has the shape of a solid plug of tissue composed of a few cells arranged radially about a central axis (*T.R.*). The nuclei are at the inner ends of the cells. Outside of this endodermal core is the ectoderm (*Ect.*) which is, in the region of the bell-margin, of the character of gelatinous tissue, containing large numbers of rudimentary nematocysts. These inclusions and the nuclei of the cells are more numerous at the point where the tentacle is to appear than elsewhere. In the medusa, as in the polyp, the greatest activity in the formation of a new tentacle is manifested by the endoderm. According to Allman,¹⁶ in some hydroids (*Campanularia Johnstoni*, for example) the first indication of tentacle formation is the thickening of the ectoderm at the point where the tentacle is to appear. This is contrary to the condition which we have in *Gonionema*.

But to continue our description: along with the growth of the endodermal process, which is to be the core of the tentacle, the ectoderm also increases rapidly and constitutes an investment which contains within it numerous nematocysts and concretions which were scattered throughout the ectoderm at the margin of the umbrella. After the tentacle has grown out for a little distance beyond the bell-margin the cells on the upper or aboral surface become modified to form an adhesive organ (Pl. XXXIII, figs. 20 and 21). The cells over a disk-shaped area become elongated until they have the form of a thick pad (Pl. XXXIII, fig. 21). The tissue immediately around the pad grows out in a flange so that the organ becomes a vacuum-cup strongly muscular around the edge. After the tentacle has grown out to a length of six to eight millimeters and has increased in diameter considerably, the cavity of the circular canal is drawn out into it. The endodermal cells, arranged radially about the central axis, thicken until they are forced away from the centre, and a tubular cavity is left (Pl. XXXIII, fig. 21). As this process takes place first at the proximal end of the tentacle, within the tissue of the bell-margin, the cavity of the circular canal is carried out along the axis of the tentacle toward the tip. In this way the tentacle, which was originally imperforate as in the polyp, becomes hollow.

¹⁶ ALLMAN, *Monograph on the Tubularian Hydroids*.

C.—*Sense-organs*.—The origin of the sense-organs is very similar to that of the tentacles (Pl. XXXIV, figs: 24 and 25). In fact, it seems clear from a study of these processes in *Gonionema* that the sense-organs must necessarily be regarded as modified tentacles. In the case of these sensory clubs (Pl. XXXIV, fig. 25, S. C.), the endodermal tissue (*End.*) of the circular canal grows down in a plug into the ectodermal tissue (*Ect.*) of the bell-margin.

This latter becomes closely applied to the outside of the plug, as a thin investing epithelium, and it also spreads out in a thin lamella over the inner surface of the capsule which appears in the ectoderm in front of the developing club. Pl. XXXIV, fig. 25, is a drawing by Prof. Brooks from a section cut transversely across the bell-margin, showing the early stage in the formation of a sense-organ. I have not been able to demonstrate the presence of sensory hairs in the cavity of the capsule. The cells at the tip of the club soon begin to secrete the solid concretion which later attains a considerable size. The concretion is invested with a thin membranous ectodermal covering. In *Gonionema* the concretions correspond with the composition which has been given for similar structures in other medusæ—a calcium salt deposit in an organic matrix. Thus it is seen that both tentacle and sense-organ consist of an endodermal core which appears as a plug of tissue growing out from the lining of the circular canal. In each case this core becomes invested with a tunic of ectoderm which remains associated with it.

NEMATOCYSTS.

¹ In the hydra-stage the earliest appearance of nematocysts was as interstitial cells arising from either tissue-layer. Their growth in *Gonionema* is much the same as in *Cordylophora lacustris* as described by Morgenstern (1901). They are carried out on the tentacles by migration along with the ectodermal layer in which they are set. The extreme attenuation of the tentacle as it is when fully extended (fig. 14) gives an admirable chance to study the cell-elements, especially the nematocysts. The tentacle appears as a delicate rod of translucent substance, partitioned off at intervals by the transverse walls of the endoderm cells, and studded along its length with numerous glistening beadlike bodies, the nematocysts. Above each of these thread cells a palpocil projects like a thorn (Pl. XXXIV, fig. 26). The capsule has an unusual

form, long and bean-shaped (Pl. XXXIV, fig. 27). Examination with a high-power objective, focussing down into the water upon the extended tentacle, shows with considerable distinctness a ganglion cell of glistening highly refractive appearance, lying close to each nematocyst (Pl. XXXIV, fig. 27, *g.c.*). In every case this ganglion cell is situated distal to the thread-capsule, toward the free end of the tentacle (Pl. XXXIV, fig. 26). A thin strand of nervous tissue runs in each direction from the ganglion cell, toward the nematocyst proximally, toward the free tip of the tentacle distally. It is visible for only a short distance, however; soon vanishing into the ectodermal tissue, and none of its branches or terminations are to be traced. It evidently innervates the netting capsule, near the base of which it can be seen.

In the gonosome the nematocysts are carried out onto the ectoderm of the growing tentacle *in situ*, as in the larva. Further growth in the extent of the ectoderm is brought about in two ways: By multiplication of the cells already incorporated in the epithelium of the tentacle, and by immigration of the cells from the thick ectodermal pad at the base. The tissue composing the pad is peculiar in character. The cell-walls are almost or quite obliterated, and the gelatinous substance contains the cell-products already mentioned. In this whole group of medusæ the older tentacles are left stranded, as it were, by the growth of the margin of the umbrella beyond their point of origin. As they are in this way carried up on to the exumbrel surface of the medusa, the pad of ectodermal tissue grows so as to fill the space between the base of the tentacle and the bell-margin, forming a round cushion of hard tissue. In sections cut through this tentacle-pad (Pl. XXXIII, figs. 22 and 23) it is seen that the concretions which lie toward the bell-margin are more dense and homogeneous; that further inward they are somewhat less solid in appearance, spaces appearing within their outer walls; and that at the side nearest the circular canal there are great numbers of netting cells in various stages of formation. All gradations are present between the solid concretion and the netting cell (Pl. XXXIII, fig. 22). Fig. 22 was drawn by Prof. Brooks to show this condition in *Gonionema*. At the inner margin of the ectodermal pad the nematocysts lie closely packed together (fig. 22). From this breeding place they work their way out on to the tentacle along which they migrate until they reach a spot

where they are needed. In young tentacles which are still elongating the nematocysts are carried out with the ectoderm as it becomes applied to the tentacle base. But after a certain time the tentacle increases only very slowly in length and additional netting cells are needed to keep up with the increase in diameter. This migration of nematocysts has been seen and described by Murbach.¹⁷ After the capsules have become established, the ectodermal covering becomes modified to form the enidocil (Pl. XXXIV, fig. 27). The nerve connection in the enidocil is developed at an early stage.

SEXUAL ORGANS.

In minute specimens of the adult gonosome the gonads are frequently found in their first stage of development. They appear as outgrowths of the ectodermal covering of the radial canals, at first in the form of a ridge projecting downward from the radial canal into the subumbrella at a point two-fifths of the distance from the top of the bell to the margin. The rudimentary ribbon of gonadal tissue elongates in both directions from the point at which it started. Text-figure 20 shows the condition in *Olindias*, in which it is similar at first to that in *Gonionema*. The gonad thus becomes an elongated ridge of tissue which finally reaches to the extremities of the radial chimiferous tubes, and increases in depth until it hangs down like a ribbon into the subumbrella. Early in its development the ribbon is somewhat sinuous, and as the medusa attains greater diameter the convolutions become more and more numerous, and farther extended on either side of the radial canal, until ultimately the folds are packed tightly together in a solid band of tissue, which at the time of maturity is extended with sexual elements. The process of formation of the sexual organs is identical in the two sexes; it is impossible to tell whether a given individual is male or female until the sexual products begin to mature.

SUMMARY.

1. Observations on the development of *Gonionema* indicate that Haeckel's sharp distinctions between jelly-fishes which he groups in

¹⁷ L. MURBACH, 1894, Beiträge zur Kenntnis der Anatomie u. Entwick. der Nesselorgane der Hydroiden. *Archiv. f. Naturg.*, 60.

his orders "Trachomedusæ" and "Leptomedusæ" are not justified.

2. Dehiscence occurs in *Gonionema* with precise periodicity, and is definitely affected by changes in light.

3. Segmentation is total and equal; endoderm is formed by delamination of the blastomeres; a solid morula results.

4. A planula stage occurs, and later a hydra stage, in which the polyp develops first two tentacles, later a second pair.

5. Youngest medusæ and oldest polyps show marked homologies; direct metamorphosis is suggested.

6. Peculiar pathological phenomena occur, the larva living for weeks in the form of a plasmodium, with amœbiform activities.

7. Alternation of generations occurs. A non-sexual form of multiplication appears, during larval life; buds are produced which are detached as planulæ and go through the same changes as the parent.

8. The order and arrangement of tentacles in the gonosome follows a definite plan of cyclic sequence, producing a figure which is cyclically, not bilaterally, symmetrical. Tentacles and sense-organs appear at determinate points on the bell margin.

9. Histogenesis of tentacles and sense-organs shows their homology

10. The origin of nematocysts from the ectodermal pad at the base of the tentacle is described.

11. Gonads arise as enlargements by proliferation of the ectodermal subumbrellar epithelium of the radial canal.

DESCRIPTION OF PLATES XXXI-XXXIV.

The figures, except those otherwise noted, have been drawn by the author.

PLATE XXXI, Fig. 1.—Adult *Gonionema* in resting attitude; floating after a period of active swimming. 2/1.

Fig. 2.—Medusa in act of swimming; bell contracted, tentacles drawn up at the end of a forward impulse. Photographed from life. 1/1.

Fig. 3.—Photograph of medusa inverted and clinging to the bottom.

Fig. 4.—One radial canal from ripe male, showing gonad. *c*, circular canal; *r*, radial canal. 8/1.

Fig. 5.—Gonad of female, during dehiscence. 20/1.

Fig. 6.—Egg during first segmentation; cleavage furrow half completed. 570/1.

Fig. 7.—Egg during second segmentation, left hemisphere completely divided, right hemisphere in process of dividing.

- Fig. 8.—Hollow blastula seven hours after fertilization. Optical section of live egg.
- Fig. 9.—Two-layered blastula, endoderm having arisen by delamination.
- Fig. 10.—Young planula larva. *P*, posterior end, *A*, anterior end. 675/1.
- Fig. 11.—Planula larva; posterior end enlarged; endodermal cells at posterior end arranged along the axis of the larva, marking line of future coelenteron, *C*.

PLATE XXXII, Fig. 12.—Two-tentacled polyp, in section; four weeks old. *Ec*, thickened basal ectoderm.

- Fig. 13.—Polyp, four months old, with five tentacles and five oral lobes, lying in the same vertical planes.
- Fig. 14.—Polyp, five months old; in typical resting attitude, tentacles, expanded 2 mm.
- Fig. 15.—Five-tentacled polyp, showing form of coelenteron and formation of bud.
- Fig. 16.—Polyp feeding upon a worm.
- Fig. 17.—Larva twenty-three days old, exhibiting transverse fission of coelenteron and elongated hydrocaulus.
- Fig. 18.—Young medusa with twelve tentacles and four sense organs; showing spherical shape and constricted bell-margin.

PLATE XXXIII, Fig. 19.—Thirty-two-tentacled medusa with fourteen sense organs. Seventh and eighth tentacles have appeared in each quadrant except quadrant A, where eighth is lacking. Four sense organs have appeared in quadrants B and D, five in quadrants A and C.

- Fig. 20.—Tentacle-tip of medusa, showing rings of nematocysts, angle of tentacle, and adhesive organ on aboral side.
- Fig. 21.—Cross section of adhesive organ. *G.C.*, gland cells composing cement gland; *M.F.*, muscular flange. 500/1, drawn by W. K. Brooks.
- Fig. 22.—Ectodermal pad at base of tentacle. *E.P.*, ectodermal pad; *T*, tentacle; *M*, mesoglea. Radial vertical section. Drawn by W. K. Brooks.
- Fig. 23.—Transverse section, at bell margin, of base of tentacle, showing tentacle pad, *C.P.*

PLATE XXXIV, Fig. 24.—Horizontal section of bell margin at level of rudiment of tentacle, *T.R.*; *N*, rudimentary nematocysts; *N.R.*, nerve ring; *T*, tentacle; *C.C.*, circular canal.

- Fig. 25.—Radial transverse section of bell, at point of origin of sense organ, *S.C.*, showing endodermal origin; *Caps.*, sensory capsule, surrounded by ectoderm; *V*, velum. Drawn by W. K. Brooks.
- Fig. 26.—Tentacle tip of larva from above. 500/1.
- Fig. 27.—Nematocyst in detail, showing enidocil, *En.*; ganglion cell. 2000/1.